

TIME BUDGET AND PREY OF *NEPHILA CLAVIPES* (LINNAEUS) (ARANEAE, ARANEIDAE) IN SOUTHERN TEXAS

Linden E. Higgins

Department of Zoology
University of Texas at Austin
Austin, Texas 78712

ABSTRACT

From diurnal and nocturnal observations of the araneid spider, *Nephila clavipes* (Linnaeus), in two locations in Texas, old pasture and scrub forest habitat, rates of prey capture, types of prey utilized and time budgets can be estimated. This species had no preferred prey types. It was never observed in a retreat but was always at the hub except when replacing silk or molting. Spiders at both locations had similar time budgets and schedules but differed significantly in the types of prey captured and the estimated contribution of each prey type to the spider diet. Despite these differences, the number of prey and the estimated dry weight of prey captured by each spider was not different between the two locations. Compared to other araneids, *N. clavipes* in Texas captured a relatively low number of prey per hour, the prey were small relative to spider size, and web investment appeared high. *N. clavipes* may be required to hunt as much as it does because it is large relative to the insects upon which it preys.

INTRODUCTION

Many spiders that build orb webs must renew the orb regularly. To understand how these spiders budget their time and energy resources between foraging and growth, more information is needed concerning foraging success and the expense of the materials and movement in web building. Important factors in both the time and energy budgets include the frequency of orb renewal, the frequency and efficiency of silk recycling, and the types and capture rates of prey utilized. Environmental factors such as prey size relative to spider size, predation and climate may influence the time spent at the hub actively hunting. Opposition of predation pressure and the need to hunt may have played a role in the evolution of structures placed on or around the orb, (such as stabilimenta and barrier webs, Lubin 1973, 1975; Eberhard 1973; Tolbert 1975), of hunting at night (A. Mahler pers. comm.) and of hunting from a retreat. During the summers of 1983 and 1984 I surveyed the diurnal and nocturnal activities of individual *Nephila clavipes* (Linnaeus) in two Texas locations. Observations on time budgets and activity schedules, web-renewal behavior and prey are presented here. *N. clavipes* is a large araneid (1-3 g when gravid) with a web of two parts: a viscid orb and mazes of silk forming barriers dorsal and ventral to the spider at the hub of the orb (Robinson and Robinson 1973a). Females were observed to feed primarily on insects much smaller than themselves, renew some or all of the orb daily, and hunt nearly twenty-four hours a day.

STUDY SITES

Brazoria County.—In July, 1983, spiders were observed for twenty-one days near Sweeny, Texas (Brazoria County). *N. clavipes* occurred primarily in two habitats: scrub forest and tall grass areas in an abandoned pasture, and cut grass. Most individuals studied were in the former habitat. A major recent disturbance in Brazoria was the infestation by the imported red fire ant, *Solenopsis invicta*, that has greatly reduced the diversity of the insect fauna (J. E. Rawlins pers. comm.).

Galveston County.—In August, 1984, spiders were studied for 30 days at the University of Houston Coastal Center, Galveston County, Texas. The site is used for a study of the cultivation of Chinese tallow trees (*Sebum sebiferum*). This forms a scrub forest similar in appearance to that found in Brazoria County. There were several hived and feral honeybee colonies (*Apis mellifera*). *S. invicta* was present, but not in the densities observed at the Brazoria site. I studied *N. clavipes* where it was most dense: in the less tended stands of tallow trees and along unused roads. No other large araneids were common at either site during the study.

METHODS

The survey method followed that of Turnbull (1960) and Castillo and Eberhard (1983). Spiders along a 200 m path were checked at regular intervals throughout the observation period. Each individual was observed for approximately 15 seconds, unless unusual behavior was in progress. Each survey included all spiders along the path, between 12 and 28 spiders (Table 1). In five surveys the spiders were checked at hourly intervals. In six surveys, the spiders were checked at half-hourly intervals starting from the time the first orb was finished until the last spider had begun to remove its orb, usually 0800 to 2400. Observations between 0100 and 0800 were made at hourly intervals to determine the time of web removal and rebuilding.

During the first check of each survey, spiders were scored as hunting or not hunting. Pre-molt spiders do not appear to hunt; they are not considered in the analysis of hunting behavior and success. At each subsequent check two types of spider behaviors were scored. Of behaviors that were observed directly, the spiders were scored as sitting at the hub, sitting in thermoregulatory positions (described by Robinson and Robinson 1974), feeding, spinning or removing silk, or moving on the orb, barriers or support lines of the web. Behavior that could be deduced from physical evidence included addition or removal of orb silk (increases or decreases in the amount of silk of the orb relative to the previous observation) and prey capture. *N. clavipes* stores all prey at the hub of the orb. Except for very small insects, consumed in less than one-half hour, the prey captured over the previous half hour could be observed.

Only diurnal (0600-1900), hourly direct observations of hunting spiders were used to construct the time budgets. This restriction was necessary to eliminate the bias towards nocturnal observations in Brazoria and diurnal observations in Galveston. Both direct and indirect observations of spider behaviors were used to construct the time schedules of the various activities. At the beginning of each

Table 1.—Dates, times, time intervals and number of individuals observed in each of the prey-capture censuses. * = Diurnal censuses hourly until first spider finished spinning, nocturnal censuses hourly after last spider began removing silk.

Site	Date	Time	Intervals	N
Brazoria 1983	17 July	1830-0130	hourly	15
	19 July	0530-1830	hourly	17
	20 July	1830-0230	half-hourly	20
Galveston 1984	1 August	0630-1930	hourly	28
	4 August	1900-0300	half-hourly*	25
	8 August	0500-1830	half-hourly*	16
	10 August	1800-0300	half-hourly*	13
	15 August	0500-1830	half-hourly*	13
	17 August	1800-0100	half-hourly*	14
	21 August	0400-0500	hourly	15
23 August	0600-1100	hourly	12	

check in Galveston, the temperature, cloud cover and (in nocturnal surveys) presence of dew were recorded.

Insects observed in the orb were placed in a size class (in 2 mm increments) and when possible, the order or family was determined. Insects in the 2 mm size class were not identified and are presented as miscellaneous small insects. Dry weights for identified prey items were estimated using the equations of Schoener (1980, Table 1) for temperate insects. Schoener's equation for "total insects" was used for unidentified prey items.

Prey capture rates were calculated using only observations of hunting spiders. Individual prey capture rates were calculated as the number of prey divided by the number of hours that individual was observed. The prey capture rate for all animals in a survey is the total number of prey for that survey divided by the sum of hours of all hunting spiders observed. Within each week, the numbers of prey captured during the diurnal and nocturnal censuses were compared using paired t-tests on spiders that were present for both censuses. From the observations of five randomly selected spiders that were present at both the diurnal and nocturnal survey in each week, individual prey-capture records were compared using repeated-measure analysis. These analyses compared the four weeks at Galveston and compared the two sites. Prey capture was too infrequent to allow comparisons between individual webs or between microhabitats within a study area.

A simultaneous study of approximately 200 marked females provided background information on the sizes of the individuals, patterns of orb renewal, and the proportion of pre-molt females. These individuals were observed each morning for six days each week. Observations of prey captured have been added to the data from the surveys in the discussion of the variety of insects captured and eaten by *N. clavipes* in southern Texas. The sizes of the spiders in each location were determined by measuring either the length of the entire first leg (Brazoria County) or the length of the tibia plus patella of the first leg (Galveston County). I switched to the latter measurement as it is obtained more accurately from spiders on webs. The two measurements are correlated and the former were converted to tibia plus patella length using an allometric equation derived from preserved females (after Vollrath 1983).

RESULTS

Background population information.—Only females were observed in this study. At both sites, the spiders were approximately fifth to eighth instar (between 0.5 and 1.4 cm tibia + patella length). In Galveston, there was a shift in the distribution of sizes in the population over the month, with the smallest instars dropping out completely by the end of August, and an increasing number of mature females. The only observed causes of mortality were failed molts and, in Galveston, cannibalism between females.

One to three days before a spider molted, it stopped renewing its orb, or replaced the viscid orb with a nonviscid platform (Christenson et al. 1985; the skeleton web of Robinson and Robinson 1973b). The condition of the orb was used to judge whether or not a spider was immediately pre- or post-molt (the new orb was not usually built until the day following the molt). Pre- and post-molt spiders did not appear to be actively hunting; only one individual was ever seen to capture prey from an old orb, and prey capture is unlikely on a non-viscid platform.

At any one time in the Galveston County population, 0 to 22% of the spiders used in the surveys were premolt. Premolt females were not included in the surveys done in Brazoria County.

Time budgets and orb renewal.—The time budgets were calculated using only diurnal (0600-1900) hourly direct observations of hunting spiders' behaviors (Fig. 1). The time budgets are not significantly different between the two locations (likelihood ratio G-test, Sokal and Rohlf 1981). By 0600 all hunting spiders had some viscid spiral in place. Diurnal prey capture is definitely impossible only when a spider is moving on the barrier webs (M). The spiders moved onto the barrier webs during the day to escape a disturbance, or, rarely, to chase a kleptoparasite or a male. In both locations, the spiders could potentially capture prey 98% of the day.

Spiders replaced between one-third and all of the orb between 2200 and 1100, most completed the new portion of the orb by 0930 (Fig. 2). The amount of new silk in the orb on any day was a function of the weather of the previous day (Higgins in prep). The spiders spun the viscid spiral in concentric sections with pauses at the hub between sections. The spiders also returned to the hub if disturbed while spinning. While at the hub, a spider could capture prey and no spinning would be done until it finished feeding.

Nocturnal orb removal took place between 2200 and 0400, with peak activity at 0100 (Fig. 2). Dewfall appears important in triggering orb renewal. I compared the distribution of the initiation of orb removal over the night between nights with and without dewfall. Spiders began removing the orb significantly earlier on the evenings when there was dew fall, compared to when there was no dewfall (Chi-square = 23.39, df = 5, $p < 0.001$). Web removal by spiders that were abandoning a location may occur earlier in the night. The spider removed one-fourth to one-third of the orb in a wedge-shaped piece, then progressively enlarged the hole in a manner similar, but not identical, to the slow-removal pattern described by Carico (1986) (Higgins in prep.). Many of the radii of the orb were constructed during the orb-removal process. Orb removal could take several hours, with the spider pausing at the hub to consume the silk or to capture prey. The amount of silk removed by a spider that was abandoning a web

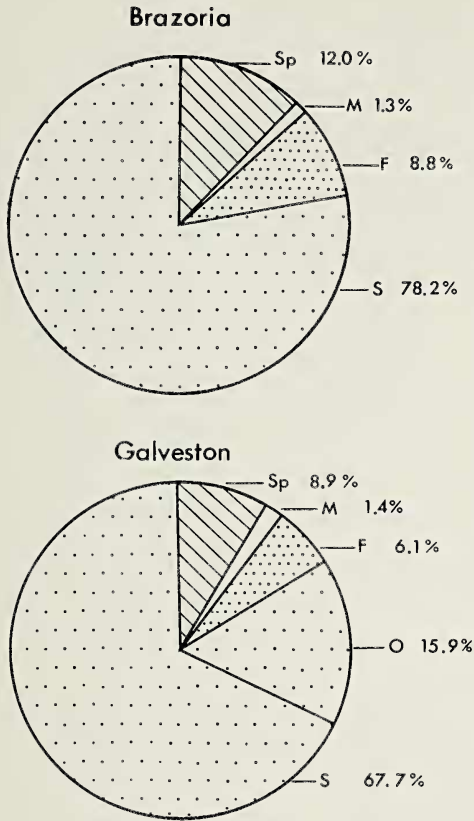


Fig. 1.—Diurnal time budget of *N. clavipes* in Galveston and Brazoria counties. S = waiting at the hub, O = thermoregulatory posture (orientation of abdomen to sun), F = feeding, S = spinning, M = moving on the barriers, frame or support strands. Prey capture was possible during all behaviors except movement off of the orb. Thermoregulatory positions were not recorded in Brazoria. The distributions are not significantly different.

site was variable, but many such spiders consumed most of the orb and barriers. Abandonment of intact webs was only seen in cases of cannibalism, heavily damaged webs, or when the spider was leaving to lay eggs. Orb rebuilding by spiders staying at the same location commenced immediately after the silk of the old orb had been consumed. Non-viscid platforms of premolt spiders were also built at this time by removal of some or all of the old orb and replacement with radii and scaffolding, but no viscid spiral. The stabilimenta were not always added at night.

During the orb removal process, most females spent some time moving on the barriers, frame and support strands. In some cases the spiders were obviously reinforcing the strands. The density of silk in the barriers was variable and was probably changed at this time.

Orb removal may occur during the day if the orb was wet by rainfall. On the one census day with rain, four of the ten actively hunting spiders removed sections of the orb when it rained, and one rebuilt a portion of the removed area after the rain had stopped. The cause of the variation in response to rainfall is unclear but appears related to the amount of water actually reaching the orb.

Prey types caught by *Nephila clavipes*.—Insects were scored as captured if they were observed to be attacked or stored at the hub, rejected if the female was observed to remove the insect from the orb, and ignored if the insect was in the orb but the spider was not observed to approach it. In Brazoria County, 90 prey-captures were recorded with 31 observations of rejected or ignored prey. In Galveston County, 164 prey-captures were recorded with no observations of

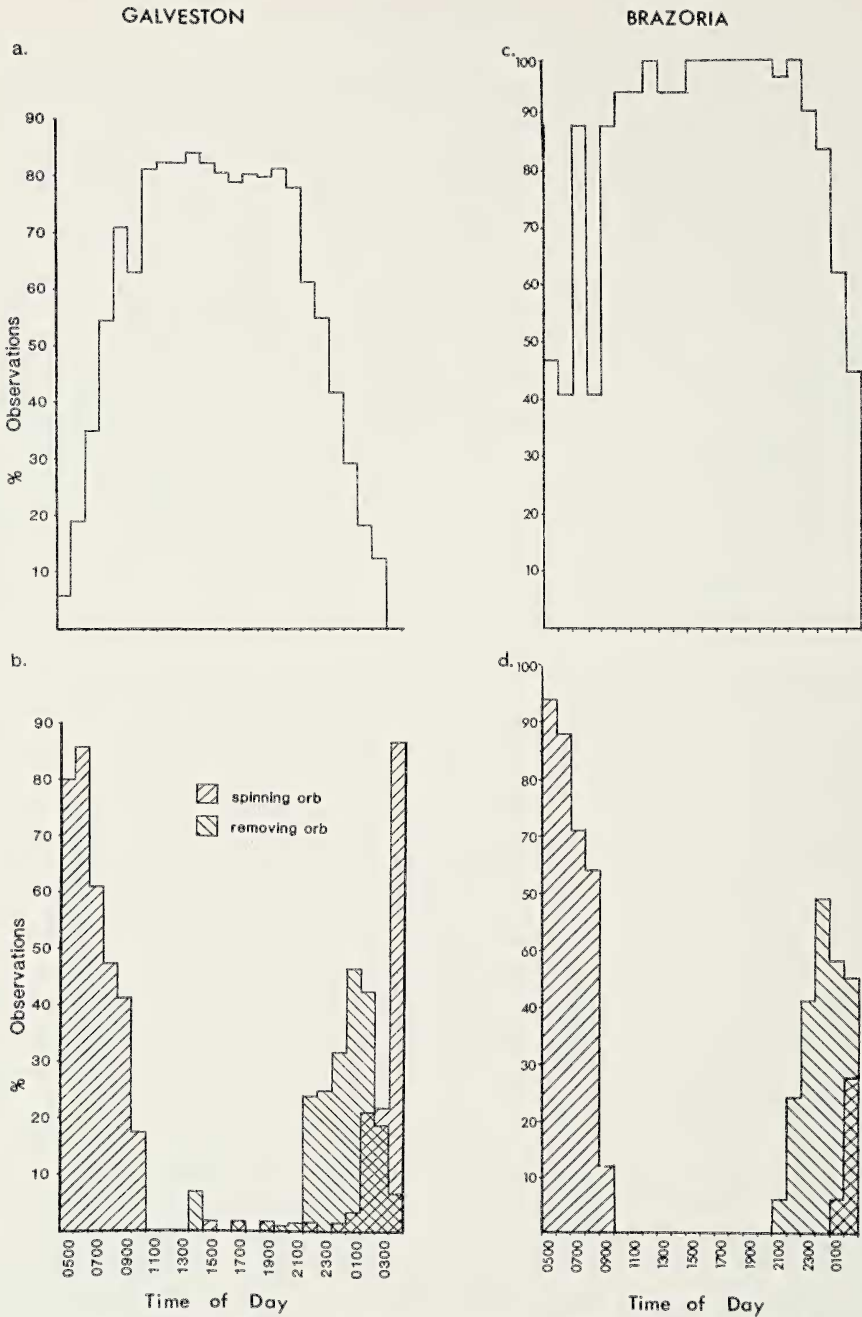


Fig. 2.—Activity schedule of female *N. clavipes* in Galveston and Brazoria Counties. The percentage of total observations is plotted against the time of day. Sunrise occurred at about 0700, sunset at about 2030: a, The percentage of individuals hunting in Galveston. At no time are all spiders hunting because of the presence of pre- and post-molt individuals in the population; b, The schedule of web renewal in Galveston; c, The percentage of individuals hunting in Brazoria. Non-hunting pre- and post-molt individuals were not used in this portion of the study; d, the schedule of web renewal in Brazoria.

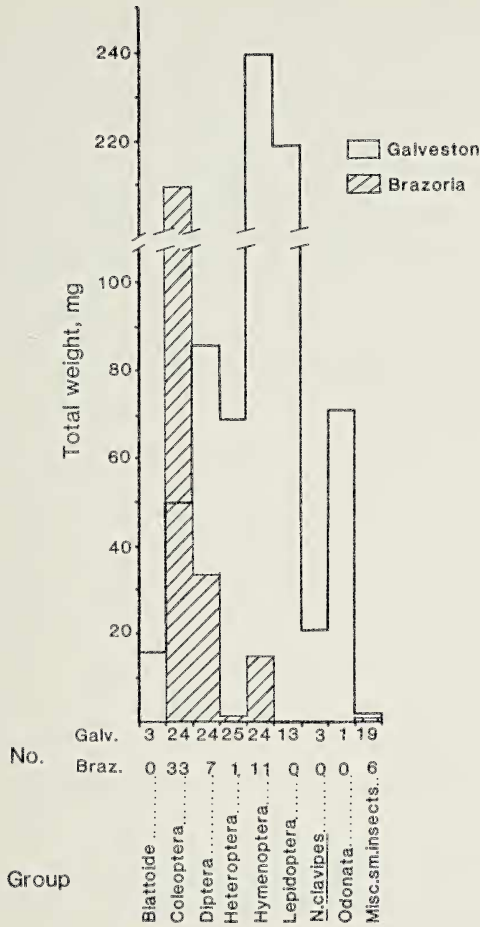


Fig. 3.—Numbers and estimated dry weights of prey identified to order. Dry weights of insects estimated from equations provided in Schoener (1980), *N. clavipes* weight estimated from weights of live spiders of equivalent size.

rejected prey. Of prey observed, 66% were identified in Brazoria County and 83% in Galveston County. The common beetles were identified to family level in Brazoria County. The numbers and estimated weights of identified prey in each order are presented in Fig. 3. Both the numbers and the weight of prey of each order are significantly different between the two locations (Chi-square for numbers of prey = 38.35, $df = 5$, $p < 0.001$; Chi-square for weights of prey = 605.2, $df = 7$, $p < 0.001$; categories with expected values of less than 1.66 were included as "Others" in the calculation of Chi-square). Lepidoptera and Hymenoptera, mostly bees, were the major sources of prey weight in the Galveston County population, whereas Coleoptera contributed the most in Brazoria County.

The histogram of body length of all observed prey (Fig. 4a) includes observations of prey capture from both the survey study and the population study. The distributions are significantly different ($G = 16.60$, $df = 7$, $p = 0.02$, lumping all prey greater than 15 mm). In both locations a large proportion of the items captured were less than 4 mm body length: 52% in Galveston and 45% in Brazoria (90% if the alate ants are included, see below). These small insects were mostly dipterans, hymenopterans and coleopterans. They contribute little to the total weight of prey captured (6% in Brazoria and 4% in Galveston, Fig. 3). The

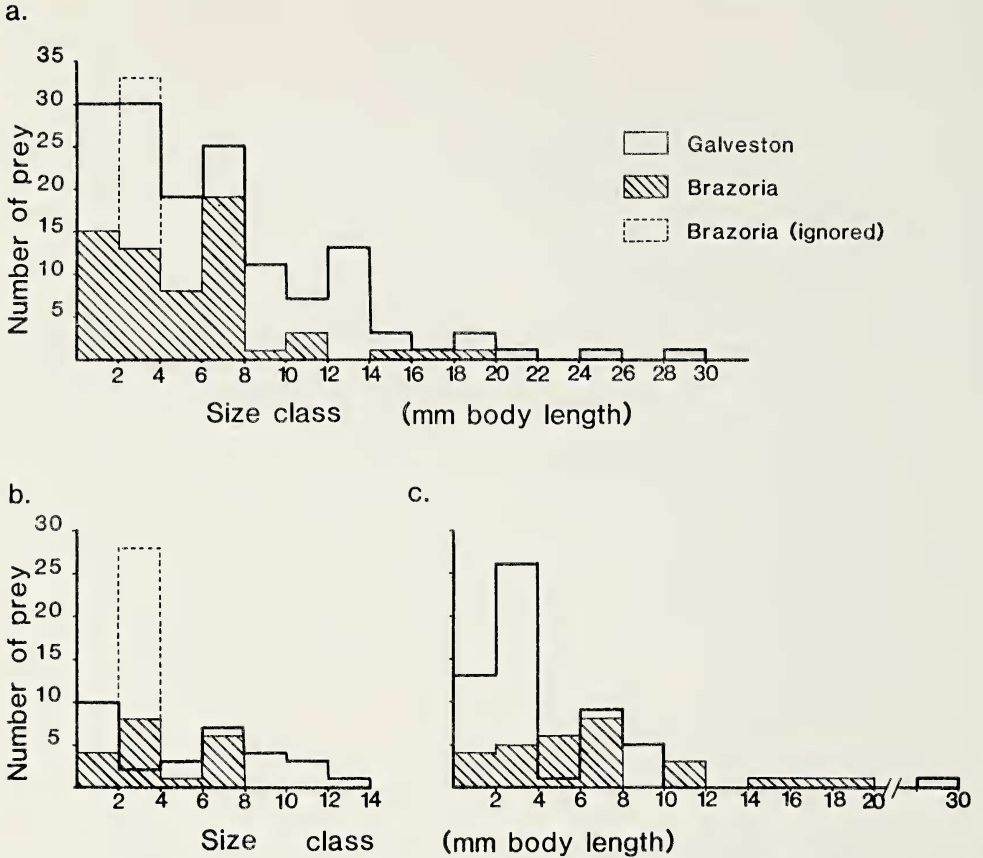


Fig. 4.—Distribution of body lengths of prey caught by *N. clavipes* at both locations. Stippled outline indicates the alate ants observed in the orbs (but ignored by the spiders) in Brazoria County: a, all prey captured; b, diurnal surveys only; c, nocturnal surveys only.

distributions of prey body lengths observed in the diurnal and nocturnal surveys are presented in Figs. 4b, c. A G-test of independence (Sokal and Rohlf 1981) was done to compare the effects of time (diurnal or nocturnal) and locality on the distribution of prey sizes. The three-way interaction of time, site and prey size was significant ($G = 25.68$, $df = 4$, $p < 0.001$). The sizes of prey are significantly different between diurnal and nocturnal surveys at each location ($G = 30.09$, $df = 8$, $p < 0.001$) and the locations are significantly different at each time ($G = 32.68$, $df = 8$, $p < 0.001$). These interactions can be partly explained by the differences in the types of prey observed at the different sites. The diurnal prey in Galveston County (bees, large Diptera, Lepidoptera) were larger than the nocturnal prey (small Coleoptera and Diptera). In Brazoria County, the diurnal prey (alate ants and Diptera) were smaller than the nocturnal (scarabs and other beetles).

N. clavipes showed individual variation in response to small (less than 4 mm) and potentially dangerous insects. During the diurnal survey in Brazoria there was an emergence of 3-4 mm alate ants, and while three spiders ignored them, another ate them immediately. Only five of 33 alates observed in orbs were eaten by spiders during the survey. The ignored alate ants were observed both escaping and being eaten by kleptoparasites; it is doubtful many of these small insects would still be in the orb when the spider removed and consumed it at the end of

the day. The spiders in Galveston County were often observed removing insects of less than 2 mm body length from their orbs. In addition, two spiders in Brazoria rejected (removed from the orb) 5-6 mm wasps that were captured by other spiders, and one female "ignored" a 30 mm beetle that did a lot of damage as it removed itself from the orb.

Prey-capture rates.—*N. clavipes* required at least one half-hour to consume most insects. Significantly more prey captures were observed when observations were done at half-hour rather than hour intervals in Galveston (paired t-test $t = 2.03$, $df = 10$, $p < 0.05$), with no change in the size range of prey observed. The smallest size class of prey is underestimated with either schedule, but I assumed that prey of less than 2 mm body length were not energetically important to the diet even though they may be numerically important (Kajak 1965; Nyffler and Benz 1978).

The pattern of prey capture over twenty-four hours was similar at both sites (Fig. 5). Potentially, the spider can capture insects any time there are viscid strands in place. However, in Galveston County, all observed prey captures occurred between 0500 and 2300, with most occurring between 0800 and 2200. In Brazoria County, all but one of the prey captures observed occurred between 0600 and 2400 (Fig. 5). The rate of prey capture was almost constant through the day and peaked at dusk (1900 to 2200). In Galveston, this peak corresponded to the evening drop in temperature (Fig. 5). This may reflect an increase in the number of flying insects, as Buskirk (1975) observed in Costa Rica. The distribution of prey capture was similar in Brazoria County, with an additional small increase in prey capture between 1100 and 1300, due in part to the alate ants.

Considering only the surveys done at half-hour intervals, the diurnal and nocturnal prey-capture rates were not significantly different within weeks in Galveston (paired t-test). Prey capture was highly variable from web site to web site; between 47 and 73% of the spiders captured prey during any one survey (considering only surveys done at half-hour intervals). The variation between individuals was greater than the variation between Brazoria and Galveston, or between weeks at Galveston County. There was no indication at either site of a relationship between prey capture and web-site tenacity.

In Galveston County, an average of 24% of the spiders captured at least one prey item greater than 4 mm body length during a single survey (32% during diurnal observation periods and 19% during nocturnal observation periods). The prey-capture rate of prey items greater than 4 mm body length was approximately half that of the total prey-capture rate (0.03 prey items per spider per hour, diurnal or nocturnal).

In Brazoria County, the nocturnal prey capture rate was higher than the diurnal prey capture rate. This is the opposite of Galveston County (Table 2). A higher proportion of spiders captured prey in Brazoria than in Galveston (Chi-square = 5.02, $df = 1$, $p < 0.02$). In Brazoria, 45% of the spiders captured prey equal to or larger than 4 mm during any one survey (29% during diurnal observations, 53% during nocturnal observations). The diurnal prey-capture rate for insects greater than 4 mm was the same as in Galveston (0.03 prey items per spider per hour), but the nocturnal rate was almost double (0.07 prey items per spider per hour).

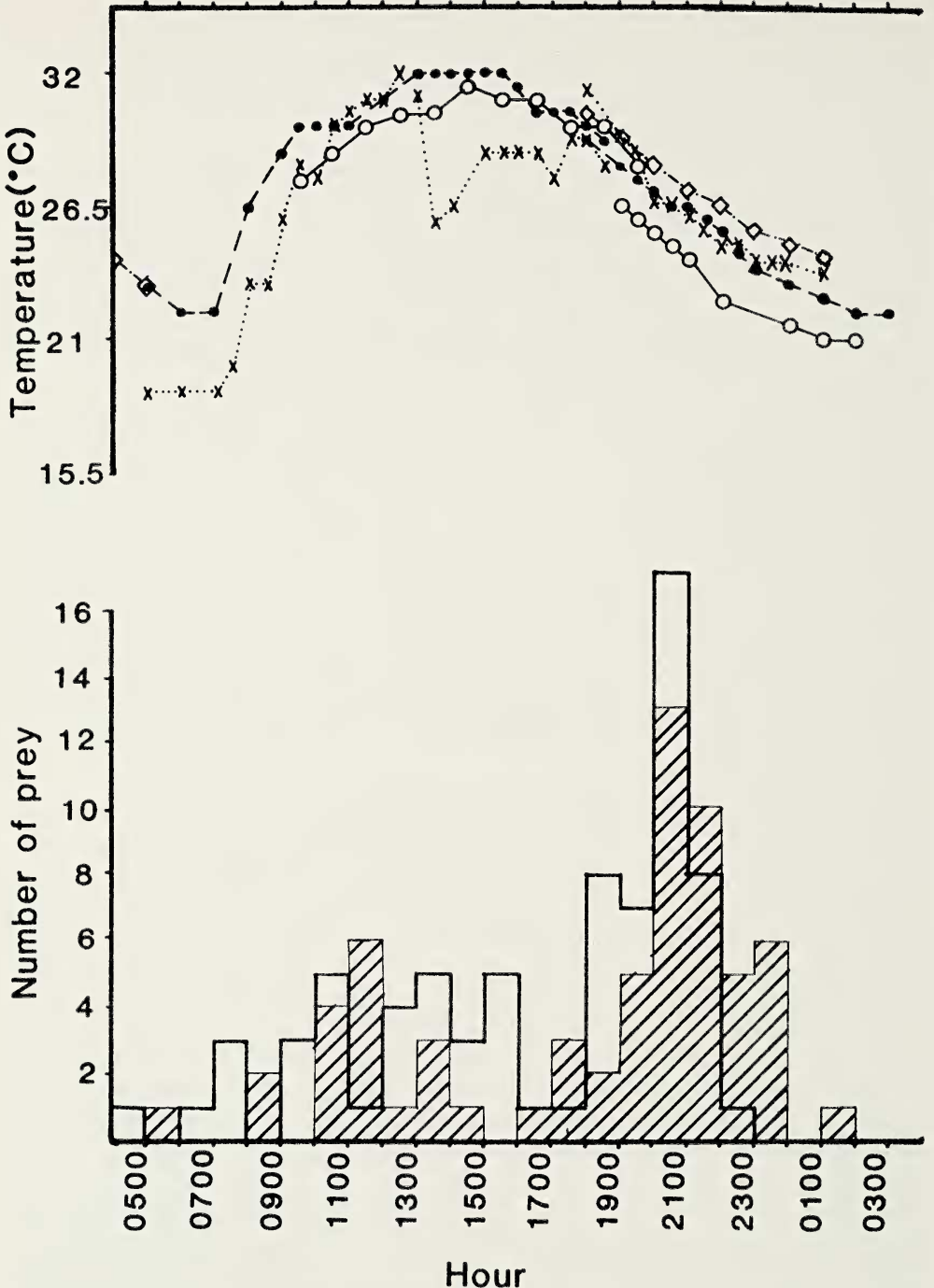


Fig. 5.—Prey capture in both locations and temperatures in Galveston County. *Brazoria* is hatched, Galveston is clear. Ignored prey are not included (see text). Temperature lines as follows: open circles = Aug 1, 4; black circles = Aug 8, 10; X·X = Aug 15, 17; diamonds = Aug 21, 23.

The total weight of prey captured by each spider during each survey was calculated (Fig. 6). I used only the data from the Galveston surveys done at half-hourly intervals but all of the *Brazoria* surveys. A total of 228.2 mg of prey were

Table 2.—Prey capture rates (number of prey captured per spider) observed in Brazoria County, July, 1983, and Galveston County, August, 1984. Overall prey-capture rates are based on 12 hour days and 10 hour nights. The rates for Galveston County are calculated using only the data from surveys done on half-hour intervals.

Place	Time	Spider-hours	Number of Prey	Prey Capture Rates	
				Per Hour	Per Survey
Brazoria	Diurnal	255	19	0.075	0.894
	Nocturnal	270	29	0.107	1.07
	OVERALL	525	48	0.091	—
Galveston	Diurnal	294	20	0.068	0.816
	Nocturnal	334	45	0.135	1.35
	OVERALL	628	65	0.104	—

observed caught in Brazoria County (50 spiders, 53 prey items), and 164.0 mg in Galveston County (67 spiders, 56 prey items). There were no significant interactions between the three factors of time of day, site, and mg prey captured (G-tests). Therefore, the between-site difference in prey sizes does not affect the estimated dry-weight of prey captured by a spider during a survey.

DISCUSSION

The activity schedules and time budgets of *N. clavipes* in the two locations in southern Texas are the same. The patterns of orb renewal are the same and are similar to those observed in the tropics for *N. clavipes* (pers. obs.) and *N. maculata* (Fabricius) (Robinson and Robinson 1973a). *N. clavipes* in southern Texas appears to have a wide range of acceptable prey. The prey caught are dependent upon the geographic location and probably also upon the microhabitat of the individual spider (Brown et al. 1985). The large number of small prey in the diet of the Texas populations is similar to the diet in studies of *N. clavipes* in Louisiana (Brown et al. 1985) and Peru (Rypstra 1985).

Web renewal and recycling.—The spiders were unable to capture prey only a short period of time each night. The length of time was dependent on whether the spider replaced all of the orb or only a section; in the former case there was a period of one or two hours when there was no viscid silk, in the latter, there was always some viscid silk. Hunting spiders are believed to respond to moving insects in the orb anytime they are not satiated. Even when not hunting, *N. clavipes* remains at the hub of the orb, and that is where molting occurs.

Web renewal patterns have not been studied in most araneids, and the extent and efficiency of silk recycling are not known. Although silk recycling has been carefully studied in *Araneus diadematus* Clerck (Breed et al. 1964; Peakall 1971; Peakall and Witt 1976) and is here reported for *N. clavipes*, it is known that there are araneids which either abandon the orbs or remove them and discard the silk (M. Robinson, pers. comm.; pers. obs.). This may be more common among the araneids with reduced orbs (Robinson and Robinson 1975) and the uloborids, with non-viscid orbs (Eberhard 1971). Web renewal and silk recycling patterns are important for understanding the evolution of foraging behavior within araneid species (Lubin 1973) and between araneids and other web-dependent spiders (Janetos 1982).

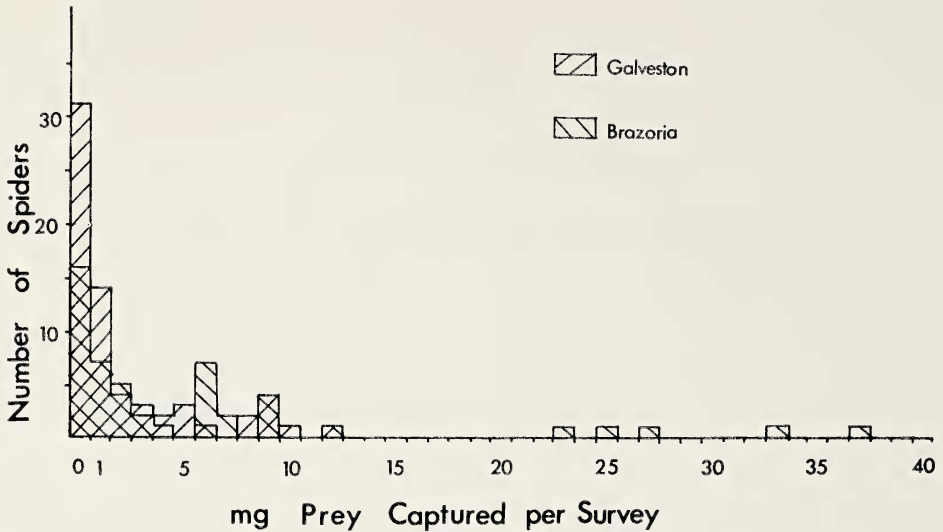


Fig. 6.—The frequency distribution of mg prey captured per spider per survey. There is no interaction between the time of the survey (diurnal or nocturnal), the location and the amount of prey captured (G-test for the 3-way interaction = 3.85, 4 df, ns; G-test for each of the 2-way interactions also not significant).

Prey captured.—The main difference between the two sites is the types of prey taken. The numbers and weights of each prey type are significantly different between sites (Fig. 3). These differences indicate that, like other web dependent spiders studied in several locations or over long periods of time, *N. clavipes* will take most common insects (Kajak 1965; Turnbull 1960; Robinson and Robinson 1970, 1973a; Nyffler and Benz 1978; Olive 1980). *N. clavipes* does not specialize on any one prey type (see also Turnbull 1960; Wise and Barata 1983) or size range (Olive 1980, Nentwig and Wissel 1986). However, the variable response to small Hymenoptera reflects selectivity by individuals (Castillo and Eberhard 1983). In Brazoria, most of the spiders ignored the alate ants and small wasps that were common during the diurnal census, but in Galveston *N. clavipes* consumed most insects caught in the orb regardless of size. This may be an indication of energetic stress in Galveston. Antagonistic interactions have been reported by Rypstra (1985) in response to artificially reduced food levels. Interactions such as female-female cannibalism and female-female and male-female displacement were common on Galveston but not at Brazoria, and may be additional indications of energetic stress.

Part of the between-size difference in prey types caught probably reflects differences in prey availability between the two locations. No samples were made of prey availability because of the difficulty in sampling insect types used by spiders (Kajak 1965; Robinson and Robinson 1973a; Uetz et al. 1978; Castillo and Eberhard 1983). The prey captured by *N. clavipes* in Galveston County were taxonomically diverse (Fig. 3). Of the orders reported as prey of other araneids, only Orthoptera were never observed. The main prey types (Diptera and Hymenoptera) were also caught by *N. clavipes* in Panama (Robinson and Mirick 1971). In contrast to the observations from Brazil (Vasconcellos-Neto and Lewinsohn 1986) and Panama (Robinson and Mirick 1971), Lepidoptera were not common prey in Texas but the contribution to the diet (estimated dry weight) was

Table 3.—Results of Chi-square and rank-order tests on prey types captured for between-site differences within species. Chi-square tests were computed over all prey types for contingency tables with smallest cells lumped into "Others". Species: *A. a.* = *Araneus quadratus*, *A. c.* = *Araneus cornutus*, *A. b.* = *Argiope bruennichi*, *N. c.* = *N. clavipes*. Sources: 1. Kajak 1965, table 3. 2. Nyffler and Benz 1978, tables 1, 2, and 3. 3. Present Study. * = Data presented only as percentages and totals. Data presented here are estimates; total absolute difference over the four stations between these totals and original totals = 4. ** = Rank order test not computed because ranks are identical. *** = Rank order test not computed because of large number of ties.

	Species				
	<i>A. a.</i>		<i>A. c.</i>	<i>A. b.</i>	<i>N. c.</i>
Location					
(Source)	Poland (1)	Switzerland (2)	Poland (1)	Switzerland (2)	U.S.A. (3)
Number of Sites	3	1	3	5*	2
Total Prey Obs. at each site	44, 34, 47	173	131, 199, 299	873, 377, 244, 215, 90	90, 164
Chi-square	19.56 (Poland)	32.9 (both)	60.3	179.5	38.35
df	8	9	8	16	5
P	<0.025	<0.001	<0.0015	<0.001	<0.001
Rank-order Test	**	$t = 4.6, ns$	**	$W = 0.431, \chi^2 = 17.24$ $df = 8, p < 0.05$	***

high. The large number of Heteroptera and honeybees in Galveston reflects the abundance of heteropteran pests found on the Chinese tallow trees (W. Shield, pers. comm.) and the honeybee hives at the research station. The diversity of prey captured in Brazoria County is lower than in Galveston County and probably reflects reduced insect diversity due to fire ant predation (J. E. Rawlins, pers. comm.). The most common prey by number and weight in Brazoria are coleopterans (40% of total prey, 80% of weight); many of these are large, nocturnal beetles (Scarabeidae, Elateridae and Lampyridae). Large beetles were never observed in the webs of *N. clavipes* at the Galveston site and are not reported as common prey in New Orleans (Brown et al. 1985) or in Panama (Robinson and Mirick 1971).

As comparison with other interpopulation studies of araneid foraging, Table 3 presents statistical analysis of published prey lists. All between-site differences in numbers of prey captured by one species are significant (Chi-square tests). In these studies as in the current study, the spiders are taking different proportions of the various prey types at different sites, however all but *N. clavipes* rank the prey types in the same order (Kendall's tau and Kendall's Coefficient of Concordance, Siegel 1956).

Most observations of other Araneidae have indicated that large proportions of the diets consist of small insects (Kajak 1965; Nyffler and Benz 1978; Olive 1980). Kajak, and Nyffler and Benz treated small prey as unimportant since the contribution of these items to the total estimated weight of prey captured is small. In all populations of *N. clavipes* where prey records have been kept, a large proportion of the prey were of small body size. A high capture rate of small prey is possible in *N. clavipes* because the viscid spiral is closely spaced for a spider of this size (Uetz et al. 1978) (4-6 viscid strands/cm in penultimate and adult females in Texas). Nentwig and Wissel (1986) found experimentally that most spiders prefer prey of 50-80% of the spiders' body length. Few prey items recorded in these studies fall within this range (7-12 mm for a spider of tibia + patella length

Table 4.—Comparisons of prey-capture rates of different araneids. * = Prey-capture rates are underestimates due to observation methods. Kajak presents the data as prey-capture per 24 hours total time of observations not given. ** = Data given as prey-capture per spider-hour. Sources: 1 = present study. 2 = Robinson and Robinson 1973a. 3 = Robinson and Robinson 1970. 4 = Olive 1980. 5 = Kajak 1965. 6 = Buskirk 1975.

Species	Location	Source	Total Time	Prey Capture Observed	Estimated PC/Hour
<i>Nephila clavipes</i>	Texas	1	1131 spider-hours	85	0.08
<i>N. maculata</i> *	New Guinea	2	3237 web-days (24 h)	6039	0.08
<i>Argiope argentata</i>	Panama	3	2809 web-days (12 h)	4672	0.21
<i>A. trifasciata</i>	U.S.A.	4	61.5 web-hours	40	0.65
<i>Araneus trifolium</i>	U.S.A.	4	37.2 web-hours	24	0.65
<i>A. cornutus</i> *	Poland	5	24 web-hours	6.7	0.3
<i>A. quadratus</i> *	Poland	5	24 web-hours	2	0.08
<i>Metabus gravidus</i> **	Costa Rica	6	—	—	1.70

= 1 cm). Rypstra (1985) reported that in Peru 85% of the prey were no greater than 5 mm body length. Brown et al. (1985) found many small prey in the diet of *N. clavipes* in Louisiana (11 to 93%), with the exact proportion dependent upon the microhabitat. In the current study, 52% of the prey in Galveston and 45% in Brazoria were 4 mm or smaller in body length, and the proportion of spiders capturing larger prey was low. Insects that are small relative to the spider's size may be very important in the diet in these populations. It may also be that occasional capture of very large insects is important. Interestingly, these studies of *N. clavipes* prey are all of populations at the edges of the distribution of this species (Levi 1980).

The prey-capture rates observed in the two Texas populations are very similar to that calculated from the data of Robinson and Robinson (1873a) for *N. maculata* (Table 4). However, the average weight of prey captured each day by *N. maculata* is estimated as 15 mg, or 1.5 times the observed capture in Brazoria, 2.5 times that in Galveston. Therefore, *N. maculata* is capturing a larger proportion of large insects. The prey-capture rates calculated from the data of Robinson and Robinson (1973a) and calculated for *N. clavipes* (this study) are much lower than prey-capture rates estimated from data available for other araneids (Table 4). However, the former may be an underestimate as the methods of Robinson and Robinson did not allow the observation of small insects that may form a part of the diet.

N. clavipes does not easily fit into any of the foraging models proposed for web-dependent spiders (Enders 1975; Olive 1980; Janetos 1982, 1984; Rypstra 1982). *Nephila* females are large araneids (gravid females often weigh over 2 g) with large, complex webs. In theory, a large predator that is dependent upon relatively small prey should spend large amounts of time or energy searching for prey (Sutherland and Moss 1985). For orb-weaving spiders, this means increased time at the hub or increased energy invested in the orb, both observed in *N. clavipes*.

Comparison of this study with studies of smaller araneids provides insight into the possible relationship between prey capture and hunting time. *Metabus gravidus* (Cambridge) has the highest per-hour capture rate reported for orb-building spiders (1.70 items per spider per hour, Buskirk 1975). Buskirk found

that *M. gravidus* individuals spent between three and eight hours hunting. The time spent hunting by each individual was inversely correlated with its hunting success on the previous day. Eberhard (1973), studying *Uloborus diversus* (Marx), found that web construction was inversely related to the frequency of prey capture. Other researchers have observed orb-web spiders without webs, found in retreats in the vegetation (Kajak 1965; Eberhard 1971, 1973; Nyffler and Benz 1978; Olive 1980; A. Mahler pers. comm.; pers. obs.). By comparison, *N. clavipes* was always found at the hub of the orb, even when molting. Other large araneids such as *N. maculata* (Robinson and Robinson 1973a), *Cyrtophora moluccensis* (Doleschall) (Lubin 1973), *Araneus cornutus* Clerck and *A. quadratus* Clerck (Kajak 1965; Nyffler and Benz 1978) were observed to hunt most of the time; how many other orb-weaving spiders are on the orb nearly 24 hours per day is unclear. The spiders' position at the hub increases its exposure to potential predators. (Predators on *N. clavipes* are not common in the temperate locations (Moore 1977; pers. obs.) but are very common in the tropical locations (pers. obs.)). These species are reported to either hunt from retreats (many *Araneus* species) or build barrier webs (*N. clavipes*, *N. maculata* and *C. moluccensis*). Hunting from retreats or building auxiliary web structures such as stabilimenta and barrier webs may have evolved in large araneids to maximize hunting time in the presence of predators.

ACKNOWLEDGMENTS

I thank my advisors R. Buskirk and M. Singer; T. Christenson, C. Craig, W. Eberhard, J. Garcia Guzman, R. Gillespie, G. Mora, D. Winsor, and H. Wolda, who read and commented upon various stages of the manuscript; K. McGuinness for help with the statistical analyses; L. Gilbert for the use of his property in Brazoria County; the University of Houston Coastal Center, especially G. Cameron. Monetary assistance was provided by a University of Texas at Austin Graduate Studies Fellowship and a Sigma Xi Grant-in-Aid of research.

LITERATURE CITED

- Breed, A. L., V. D. Levine, D. B. Peakall and P. N. Witt. 1964. The fate of the intact orb web of the spider *Araneus diadematus*. *Cl. Behaviour*, 23:43-60.
- Brown, S. G., E. M. Hill, K. E. Goist, P. A. Wenzl and T. E. Christenson. 1985. Ecological and seasonal variations in a free-moving population of the golden-web spider, *Nephila clavipes*. *Bull. British Arachnol. Soc.*, 6:313-319.
- Buskirk, R. E. 1975. Coloniality, activity patterns and feeding in a tropical orb-weaving spider. *Ecology*, 56:1314-1328.
- Carico, J. E., 1986. Web removal patterns in orb-weaving spiders. Pp. 306-318, *In Spiders—Webs, Behavior and Evolution*. (W. A. Shear, ed.). Stanford Univ. Press, Stanford.
- Castillo, J. A. and W. G. Eberhard. 1983. Use of artificial webs to determine prey available to orb weaving spiders. *Ecology*, 64:1655-1657.
- Christenson, T. E., S. G. Brown, P. A. Wenzl, E. M. Hill and K. C. Goist, 1985. Mating behavior of the golden-orb weaving spider *Nephila clavipes*: I. Female receptivity and male courtship. *J. Comp. Psych.*, 99:160-166.
- Eberhard, W. G. 1971. The ecology of the web of *Uloborus diversus*. *Oecologia*, 6:328-342.
- Eberhard, W. G. 1973. Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J. Zool. London*, 171:367-384.

- Enders, F. 1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). *Amer. Natur.*, 109:737-763.
- Janetos, A. C. 1982. Foraging tactics of two guilds of web-spinning spiders. *Behav. Ecol. Sociobiol.*, 10:19-27.
- Janetos, A. C. 1984. Comparative ecology of two linyphiid spiders (Araneae: Linyphiidae). *J. Arachnol.*, 11:315-322.
- Kajak, A. 1965. An analysis of food relations between the spiders *Araneus cornutus* Clerck and *Araneus quadratus* Clerck and their prey in meadows. *Ekologia Polska—Seria A.*, 13:1-46.
- Levi, H. W. 1980. The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bull. Mus. Comp. Zool.*, 149:1-75.
- Lubin, Y. D. 1973. Web structure and function: the nonadhesive orb-web of *Cyrtophora moluccensis* (Araneae: Araneidae). *Forma et Functio*, 6:337-358.
- Lubin, Y. D. 1975. Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae: Araneidae) on Daphne and Santa Cruz Islands, Galapagos. *J. Arachnol.*, 2:119-126.
- Moore, C. W., 1977. The life cycle, habitat and variation in selected web parameters in the spider *Nephila clavipes*. *Amer. Midland Natur.*, 98:95-108.
- Nentwig, W. and C. Wissel. 1986. A comparison of prey lengths among spiders. *Oecologia (Berlin)*, 68:595-600.
- Nyffler, M. and G. Benz. 1978. Die Beutespektren der Netzspinnen *Argiope bruennichi* (Scop.), *Araneus quadratus* Cl. und *Agelena labyrinthica* (Cl.) in Odlandwiesen bei Zurich. *Rev. Suisse Zoologie*, 85:747-757.
- Olive, C. 1980. Foraging specializations in orb-weaving spiders. *Ecology*, 61:1133-1144.
- Peakall, D. B. 1971. Conservation of web proteins in the spider *Araneus diadematus*. *J. Exper. Zool.*, 176:257-264.
- Peakall, D. B. and P. N. Witt. 1976. The energy budget of an orb web-building spider. *Comp. Biochem. Physiol.*, 54A:187-190.
- Robinson, M. H. and H. Mirick. 1971. The predatory behavior of the golden-web spider *Nephila clavipes* (Araneae: Araneidae). *Psyche*, 78:123-139.
- Robinson, M. H. and B. C. Robinson. 1970. Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. *Zool. J. Linnaen Soc.*, 49:345-357.
- Robinson, M. H. and B. C. Robinson. 1973a. Ecology, and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contrib. Zool.*, 149.
- Robinson, M. H. and B. C. Robinson. 1973b. The stabilimenta of *Nephila clavipes* and the origins of stabilimentum building in araneids. *Psyche*, 80:277-288.
- Robinson, M. H. and B. C. Robinson. 1974. Adaptive complexity: the thermoregulatory postures of the golden-web spider, *Nephila clavipes*, at low latitudes. *Amer. Midland Nat.*, 92:386-396.
- Robinson, M. H. and B. C. Robinson. 1975. Evolution beyond the orb web: the web of the araneid spider *Pasilobus* sp., its structure, operation and construction. *Zool. J. Linnaen Soc.*, 56:301-314.
- Rypstra, A. L., 1982. Building a better insect trap: an experimental investigation of prey capture in a variety of spider webs. *Oecologia*, 52:31-36.
- Rypstra, A. L. 1985. Aggregations of *Nephila clavipes* (L.) (Araneae: Araneidae) in relation to prey availability. *J. Arachnol.*, 13:71-78.
- Schoener, T. W. 1980. Length-weight regressions in tropical and temperate forest-understorey insects. *Ann. Entomol. Soc. Amer.*, 73:106-109.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill Kogakusha, Ltd. London.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry. The Principles and Practice of Statistics in Biological Research*, Second Ed. W. H. Freeman and Co., San Francisco.
- Sutherland, W. J. and D. Moss. 1985. The inactivity of animals: influence of stochasticity and prey size. *Behaviour*, 92:1-8.
- Tolbert, W. W. 1975. Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). *Psyche*, 82:29-52.
- Turnbull, A. L. 1960. The prey of *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). *Canadian J. Zool.*, 38:859-873.
- Uetz, G. W., A. D. Johnson and D. W. Shemske. 1978. Web placement, web structure and prey capture in orb-weaving spiders. *Bull. British Arachnol. Soc.*, 4:141-148.

- Vasconcellos-Neto, J. and T. M. Lewinsohn. 1985. Discrimination and release of unpalatable butterflies by *Nephila clavipes*, a neotropical orb-weaving spider. *Ecol. Entomol.*, 9:337-344.
- Vollrath, F. 1983. Relative and absolute growth in *Nephila clavipes* (Arachnida: Araneae: Argiopidae). *Verh. naturwiss. Ver. Hamburg.*, 26:277-290.
- Wise, D. H. and J. L. Barata. 1983. Prey of two syntopic spiders with different web structures. *J. Arachnol.*, 11:271-281.

Manuscript received January 1986, revised May 1987.